

Impacts of climate change on forests: physiological responses of *Acer rubrum*, *Quercus rubra*, and *Populus grandidentata* to variable air and soil moisture.

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Abstract:

As climate change continues, it is vitally important to understand the complex forest-atmosphere dynamics that significantly contribute to determining atmospheric conditions and global mean temperature so that climate models can become more accurate, and climate change can be more accurately projected and, thus, planned for. As temperatures warm and precipitation patterns change, plants will undergo more frequent and severe moisture stress. This study examines whether air or soil water content has a larger effect on plant physiology, as well as how different species respond to changes in water availability. Vapor pressure deficit of the air was found to be a greater driver of physiological responses than soil moisture. Oaks (an anisohydric species) demonstrated a higher degree of response than maples (an isohydric species) did, but it is still unclear how these two water use strategies compare during periods of severe water stress.

Introduction:

The Earth is currently undergoing a period of intense and rapid global climate change. Depending on human activities, the US will see an increase of 2-11.5 degrees Celsius in the mean global temperature by the end of the century (NRC, 2010); this will impact many other aspects of the climate, both biotic and abiotic. In order to explore sensitivities of the planet and better prepare for the effects of these changes, a number of climate models have been created. These models project how different components of the Earth system will be affected based on a large number of factors. Currently, these models use a simplified parameterization for modeling plant-atmosphere interactions; for example, they treat trees as a few broad functional types, parameterizing grossly the way they give off and take in compounds to and from the atmosphere and soil.

Atmospheric properties such as humidity, temperature, and chemical composition have a large effect on potential transpiration rates, since actual root water uptake by plants results from complex interactions between roots and soil moisture at different depths, modulating water transfer from roots, to stem, and to leaves. However, different species of trees have different responses to varying climatic and atmospheric conditions, such as increased atmospheric carbon dioxide or decreased soil water availability. The differences in these physiological responses mean that a climate model that treats all forests in a given climatic zone (e.g. temperate, tropical, boreal) as the same can be quite inaccurate, especially since forests participate in a number of important climate feedback processes. For example, tropical forests participate most in climate cooling, since they create local cooling by evaporation as well as by sequestering carbon; boreal forests, on the other hand, have a local warming effect by reducing albedo by decreasing snow cover area, so although they sequester carbon they may have an overall warming, rather than cooling, effect on global climate overall. Temperate forests contain the most uncertainty about total global climate influence, since they sequester carbon, but may either decrease or increase albedo, depending on local conditions such as soil albedo, species makeup, winter snow cover, and surface roughness (Jackson et al, 2008)(Betts, 2011). Additionally, it is currently unclear how plants at the species level are

likely to respond to climate change.

Besides temperature, another important aspect of climate that is changing and will continue to change is precipitation. Although changes in precipitation are more difficult to model at a high resolution than temperature, it is certain that significant changes will occur. This will include regions that experience an increase in precipitation, regions that receive less precipitation, and a dramatic overall increase in severe precipitation events. An increase in the proportion of rain falling as heavy rather than light rain will mean a decrease in average soil moisture even if total rainfall remains the same, because heavy rain increases the amount of water lost to runoff, as well as increasing erosion; in many areas it is also projected that rainfall will tend to decrease during the growing season, when it is needed by plants, even if annual total precipitation increases (USGCRP, 2009). Although it is very difficult to project exactly how regional precipitation patterns will be affected by climate change, the increase in global mean temperature is quite certain, and this increase will drive many forests to reach moisture stress conditions due to the growth of moisture deficit in the atmosphere.

Plant moisture stress indicates water demand within a plant; the tension in the xylem of a leaf (i.e. leaf water potential) is a measure of water stress. Changing precipitation patterns will cause drought conditions in many areas due to decrease in soil moisture from increased runoff and decreased total precipitation. Even in those areas where soil moisture does not change dramatically, however, plants will still undergo increased moisture stress due to the increase in mean global temperature and the resulting increase in evapotranspiration potential. This is because the ability of an air mass to hold water increases exponentially as the air warms; since plant transpiration is driven by the difference in water potentials between the soil and the air, an increase in air moisture capacity means that plants will have a more difficult time obtaining enough moisture from the soil to make up for the increase in evaporation.

It is certain that incidence of moisture stress in forests will increase as the climate continues to change, but it is unclear how different species of trees will respond. Many species-specific

characteristics affect how trees respond to low-moisture conditions. For example, root depth varies widely between species; the root systems of aspens are generally shallower than those of maples, and much shallower than the deep-rooted oaks (Bovard et al 2005). Under extreme cases, low moisture conditions can lead to not just stomatal closure and halting of photosynthesis (and thus also a halt to carbon fixation), but also to tree mortality through xylem breakage or cavitation, and thus to extremely detrimental or even fatal tissue dehydration (Anderegg et al, 2011).

Understanding how different trees respond physiologically to changes in soil moisture is essential for the development of reliable climate models. Additionally, present modeling approaches fail to model the adaptive and spatiotemporally varying patterns of soil root water uptake, especially in heterogeneous soil moisture environments, leading to early prediction of water-constrained transpiration, and it is unclear how plant root status responds to vertically heterogeneous soil moisture conditions in the root zone and different transpiration demands. It is necessary to conduct *in situ* studies of root water potential, especially for plants that live in heterogeneous environments, since these conditions are complex, constantly in flux, and thus nearly impossible to replicate in a lab setting. This work will contribute to such understanding by inferring information on species-level responses to changing atmospheric (above-surface) and hydrologic (below-surface) conditions by measuring how leaf water potential (the amount of tension in the xylem, which is a measure of moisture stress), photosynthesis, and leaf conductance vary daily and seasonally with soil moisture; photosynthesis varies widely over the course of one day, as temperature and light levels vary, while soil moisture is relatively constant over the course of one day but tends to decline on average over the course of the growing season (James et al, 2003).

This study is intended to investigate how physiological processes and water stress status of different species of trees varies with air and soil moisture.

Methods:

The general approach for this study is to study variations in plant physiology as a function of plant water stress, and to relate soil moisture and plant water potential across a range of atmospheric conditions—from hot and dry to wet and cool.

The sample site is a 95-year-old mixed hardwood forest with sandy, well-draining soil in northern Lower Michigan; *Populus grandidentata* (bigtooth aspen) is a declining canopy dominant, while *Acer rubrum* (red maple) and *Quercus rubra* (Northern red oak) are emerging canopy dominants. *Betula papyrifera* (paper birch) is also a declining dominant species. Common understory saplings (occasionally reaching the canopy) include *Pinus strobus* (white pine), *Pinus resinosa* (red pine), *Fagus grandifolia* (American beech), and *Acer pensylvanicum* (moose maple).

Three *A. rubrum* and three *Q. rubra* trees with branches low enough to be reached by 2m scaffolding were chosen for sampling, along with three *P. grandidentata* root suckers. Root suckers are small clonal shoots, or ramets, growing on the primary roots of a parent tree, or ortet; if transpiration from root suckers is zero, leaf water potential of a root sucker is in equilibrium with the water potential at the root collar of the parent tree. Since aspen trees are generally very tall and have no low branches, root suckers are the best way to measure water potential.

Each tree was revisited every 3-4 days, with 3 trees (one of each species being studied) visited each sampling day. Samples were taken during three periods of time during the day: predawn (before photosynthesis begins and evapotranspiration is thus at a minimum: before sunrise, approximately 5:00-5:40), midday (when temperatures are greatest and nonlinearities of stomatal behavior are likely most pronounced: approximately 12:00-14:00), and late day (approximately 16:00-18:00).

Leaf water potential (LWP) was measured three times each sampling day using a PMS Instrument Company pressure chamber (precision to .001 MPa). 2 leaves were taken from each aspen root sucker and 3 leaves from the canopy bottom of each maple and oak during each round of sampling. The time, height, temperature, and relative humidity at each leaf was also recorded.

During midday and late day measuring periods, photosynthesis and conductance were measured for 3 leaves on each oak and maple tree using a LI-COR LI-6400 Portable Photosynthesis System. The same leaves on each tree were used for each LI-COR measurement, and were at similar heights as the leaves being sampled for LWP. Photosynthesis and conductance of the aspen sprouts was not measured, because root suckers get the majority of their resources (water, nutrients, carbohydrates, and hormones) from the root system of the parent tree that they are growing from. This relationship causes root sucker ramets to behave very differently than independent ortets; for example, it has been shown to reduce the age of first flowering by over a decade in *P. tremuloides* (Barnes, 1966).

Soil moisture, which varies little during a single day, was measured once each day using a HydroSense probe (20 cm depth; precision to 1%) and MiniTRASE system (30 and 60 cm depths; precision to .1%). For each tree and root sucker, soil moisture was measured at distances of 1, 2, and 4 meters from the stem in four cardinal directions. At each point, soil moisture was measured at depths of 20 and 30 cm, and at a depth of 60 cm at each of the 1 and 4 m distances.

Results:

- **Seasonal trends**

There was no overall seasonal trend for soil moisture over time for the period of study (Fig. 1). There was also no seasonal trend for leaf water potential (LWP) over time (Fig. 2).

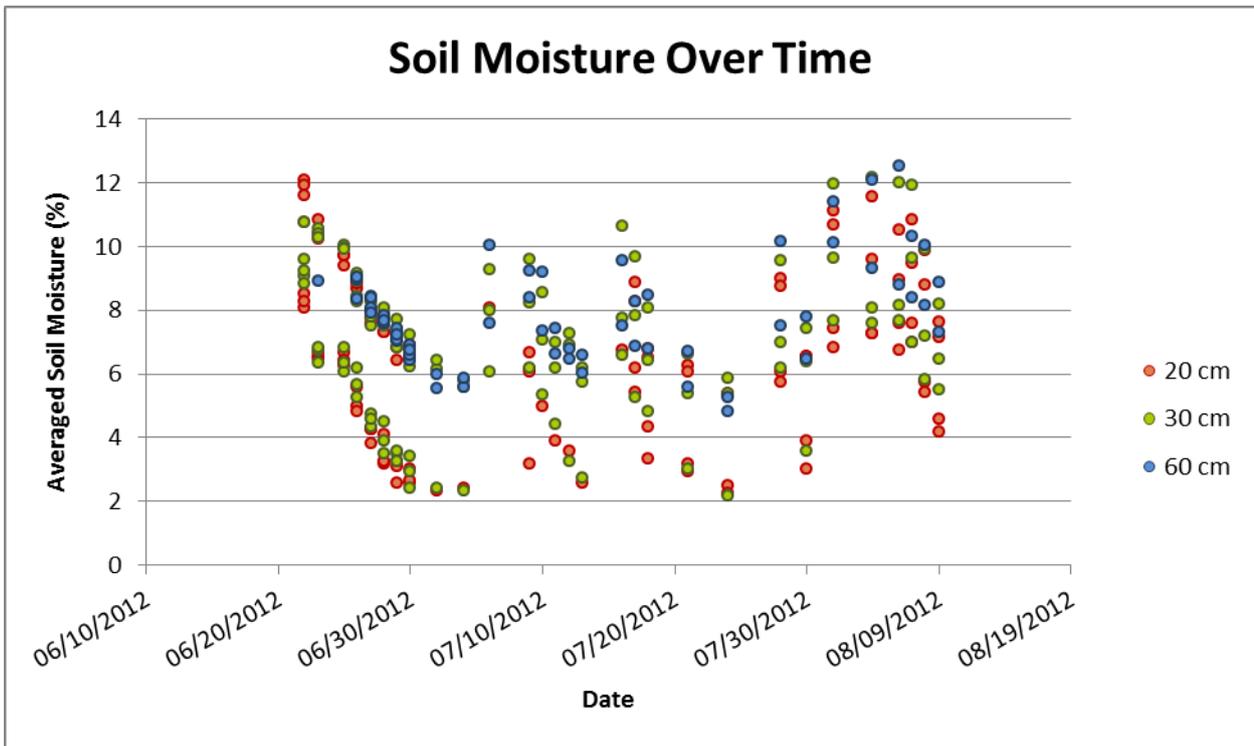


Figure 1. Soil moisture over time; there was no overall trend over the period of study.

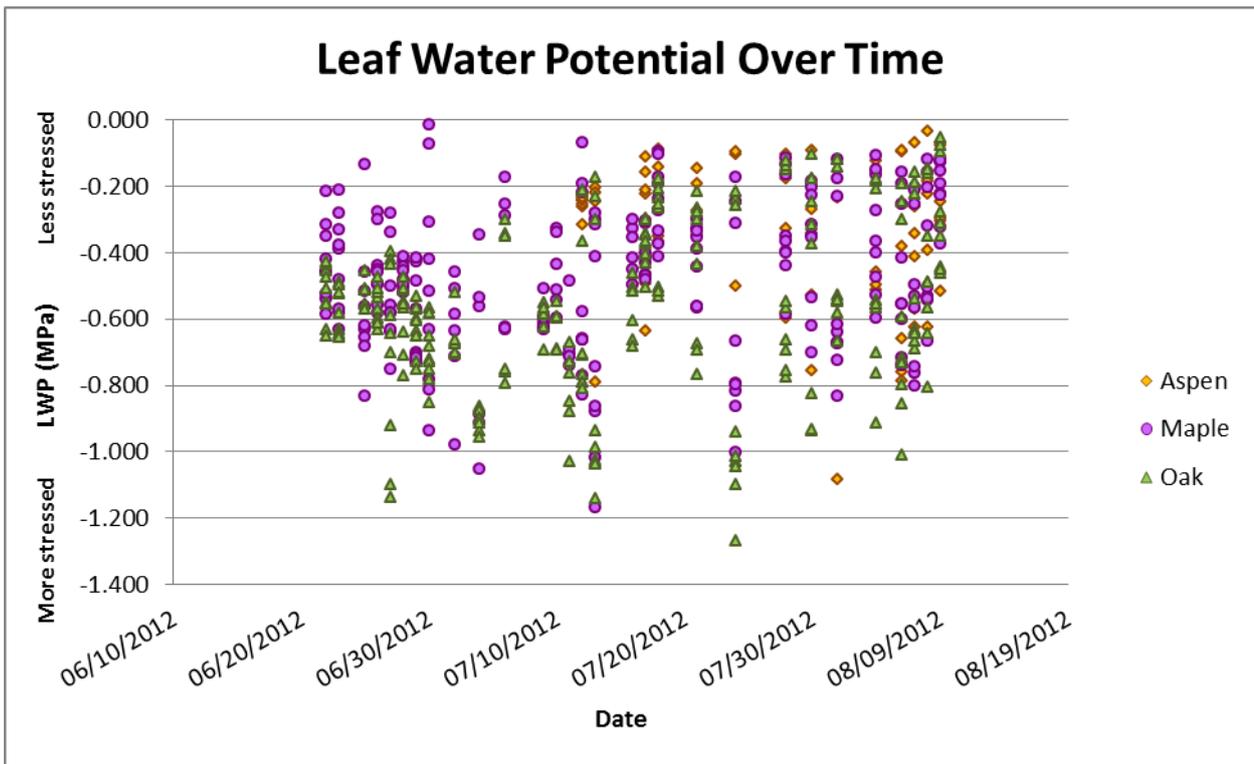


Figure 2. Leaf water potential over time; there was no trend over the period of study.

- **Soil moisture and leaf water potential**

When analyzed using a linear regression with multiple independent variables—vapor pressure deficit (VPD) and soil moisture—to assess what variation was linked to each variable as if the other had been constant, LWP and soil moisture during the predawn period were shown to be highly significantly negatively correlated for oaks ($p=.003$), but not for aspen root suckers ($p=.652$) or maples ($p=.245$) (Fig. 3). During the midday period, however, there was a significant negative relationship only for maples ($p=.011$), and a significant positive relationship for aspen sprouts ($p=.013$) (Fig. 4). Soil moisture and the midday LWP of oaks were not significantly correlated ($p=.113$). Late day measurements showed no significant relationship between soil moisture and LWP for maples ($p=.855$) or oaks ($p=.839$), but a significant positive correlation for aspen sprouts ($p=.006$) (Fig. 5).

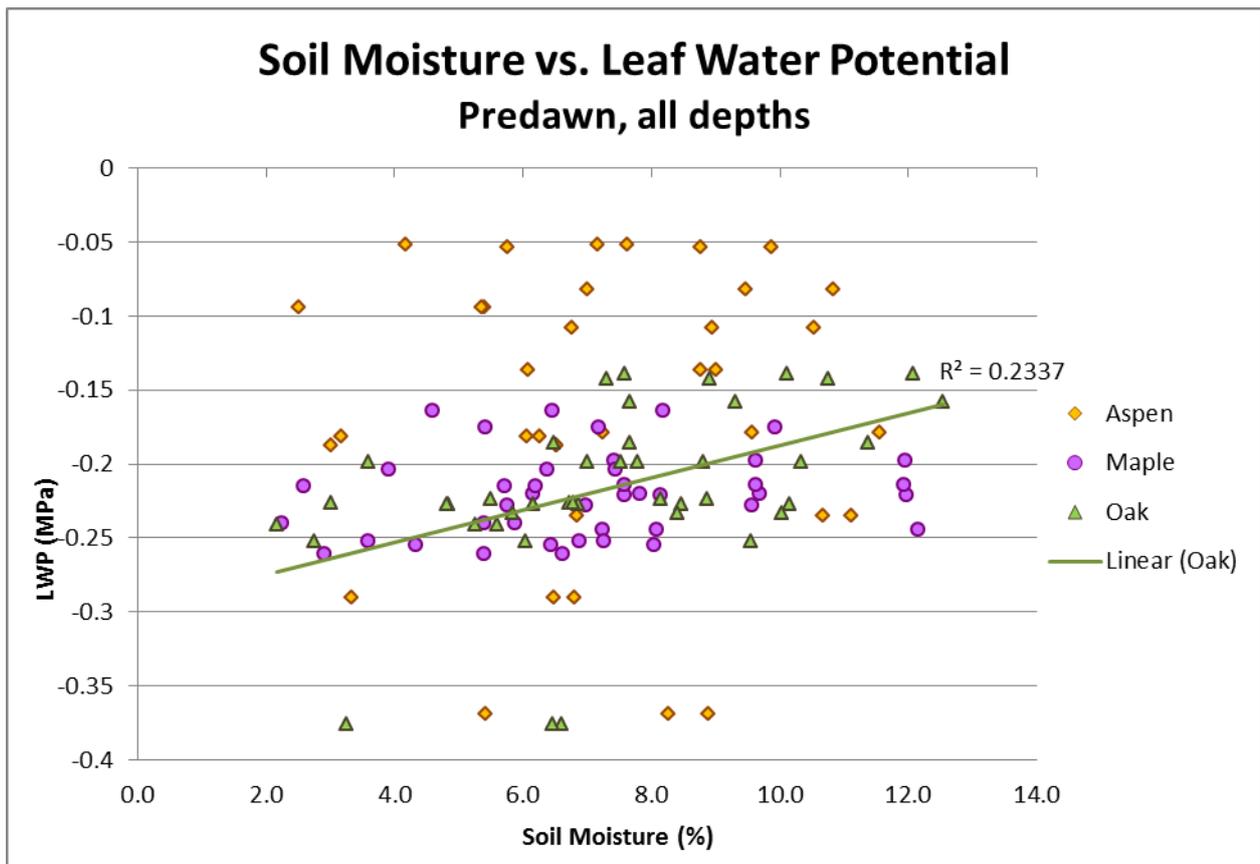


Figure 3. Predawn soil moisture and LWP. Linear regressions were analyzed for significance with variation due to VPD removed, but this graph shows the actual measured variation; significant relationships are indicated by the presence of trend lines.

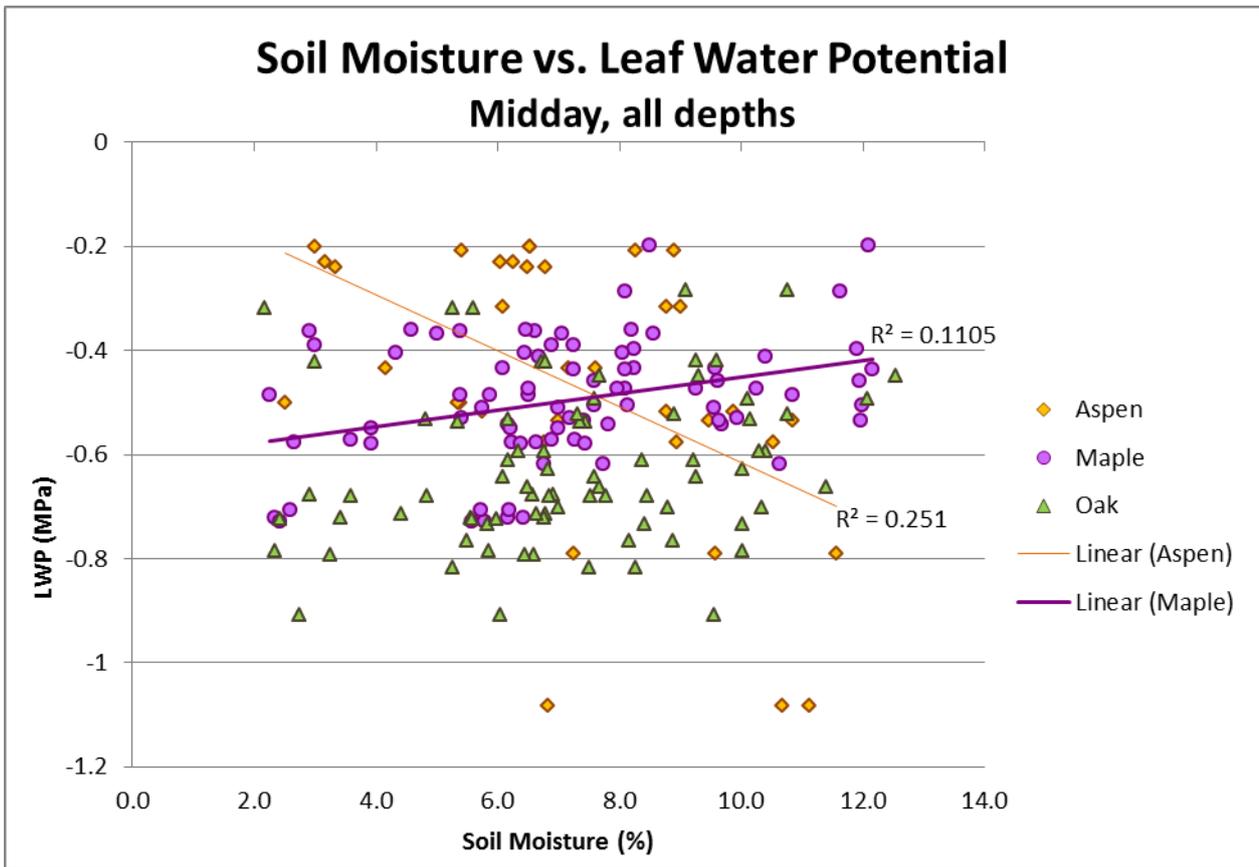


Figure 4. Midday soil moisture and LWP. Figure 3. Predawn soil moisture and LWP. Linear regressions were analyzed for significance with variation due to VPD removed, but this graph shows the actual measured variation; significant relationships are indicated by the presence of trend lines.

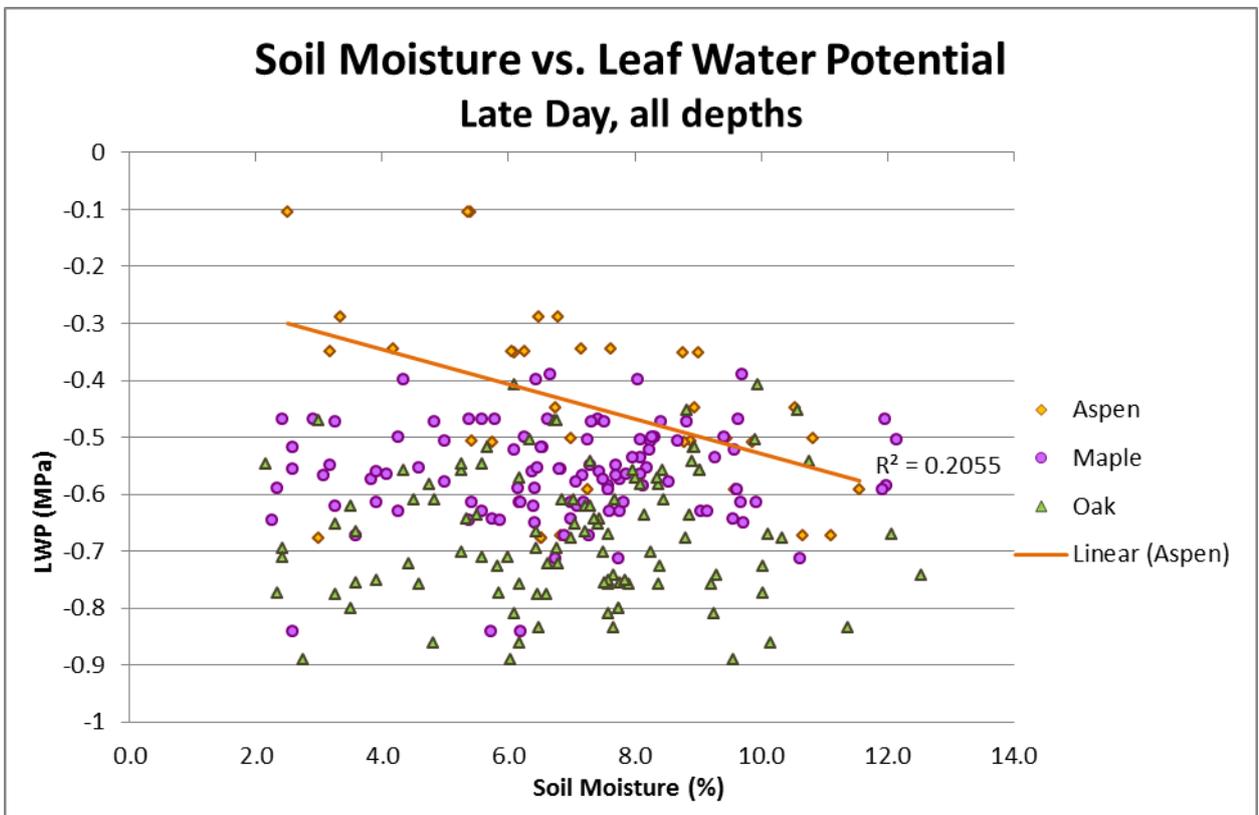


Figure 5. Late day soil moisture and LWP. Linear regressions were analyzed for significance with variation due to VPD removed, but this graph shows the actual measured variation; significant relationships are indicated by the presence of trend lines.

- **Vapor pressure deficit and leaf water potential**

LWP and VPD relationships were analyzed using linear regressions run with soil moisture as an additional independent variable to discover what variation was due to VPD as if soil moisture had been constant. For the midday time period, VPD was found to be highly significantly correlated for maples ($p=.003$) and oaks ($p<.001$), and approaching significance for aspen sprouts ($p=.057$) (Fig.6). Late day LWP and VPD relationships were highly significant for oaks ($p<.001$), significant for maples ($p=.034$), and not significant for aspen sprouts ($p=.856$) (Fig. 7).

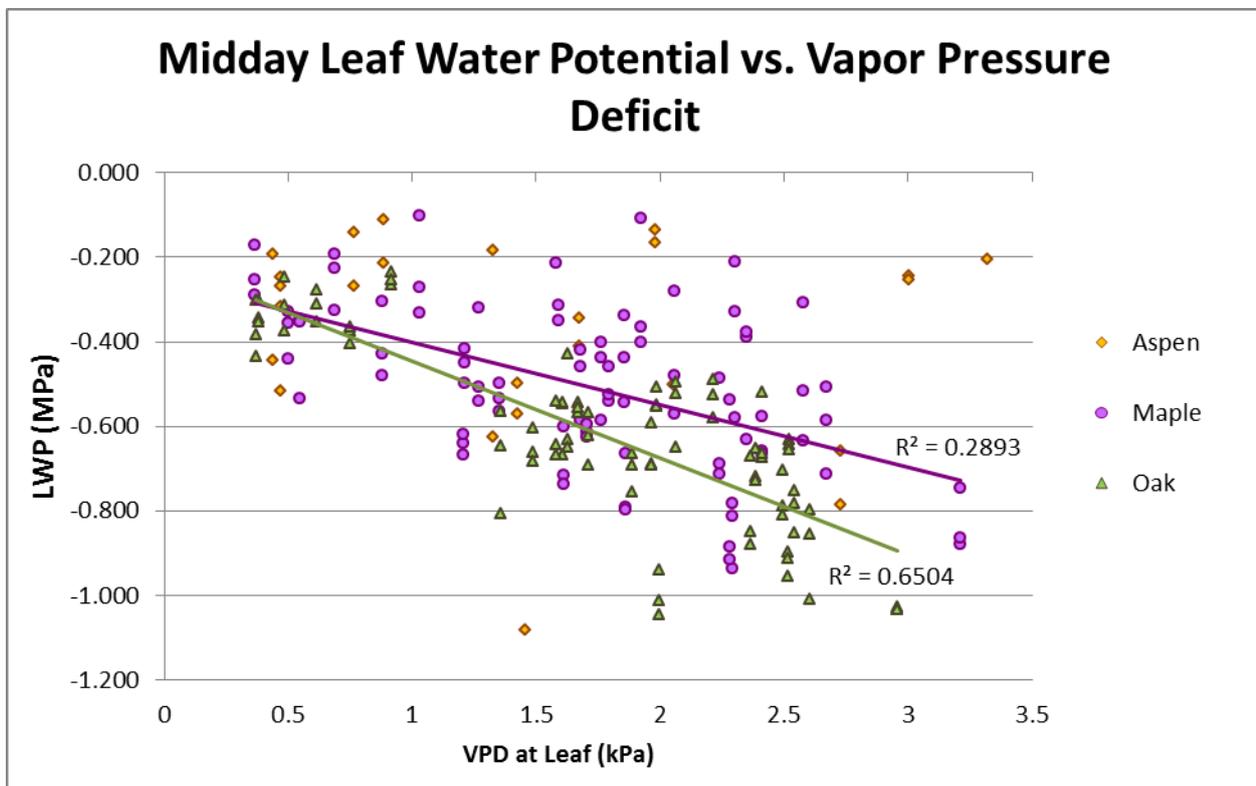


Figure 6. Midday LWP and VPD. Linear regressions were analyzed for significance with variation due to soil moisture removed, but this graph shows the actual measured variation; significant relationships are indicated by the presence of trend lines.

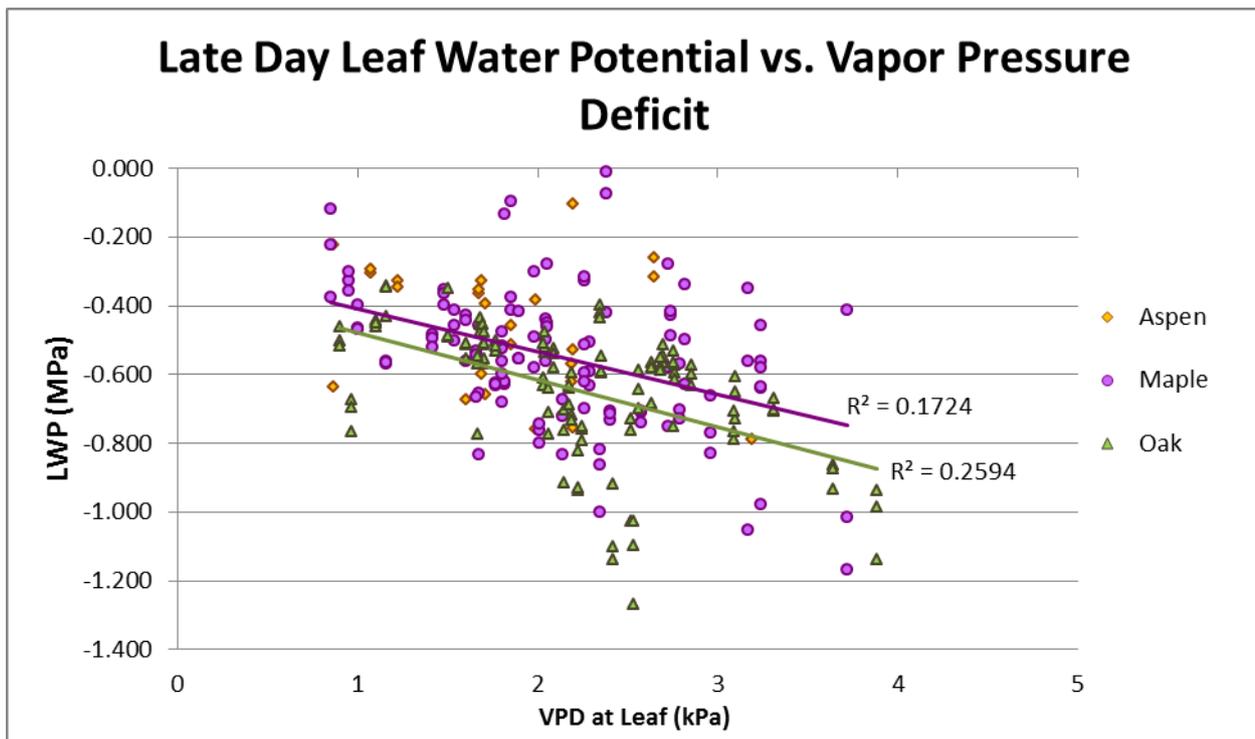


Figure 7. Late day LWP and VPD. Linear regressions were analyzed for significance with variation due to soil moisture removed, but this graph shows the actual measured variation; significant relationships are indicated by the presence of trend lines.

- **Vapor pressure deficit and conductance**

Relationships between VPD and conductance were analyzed using linear regressions that also used soil moisture and PAR as independent variables so that relationships could be analyzed without the confounding variation from these factors. Midday relationships were not significant for either maples ($p=.138$) or oaks ($.274$) (Fig. 14). During the late day time period, VPD and conductance were highly significantly correlated for both maples ($p<.001$) and oaks ($p=.001$) (Fig. 15).

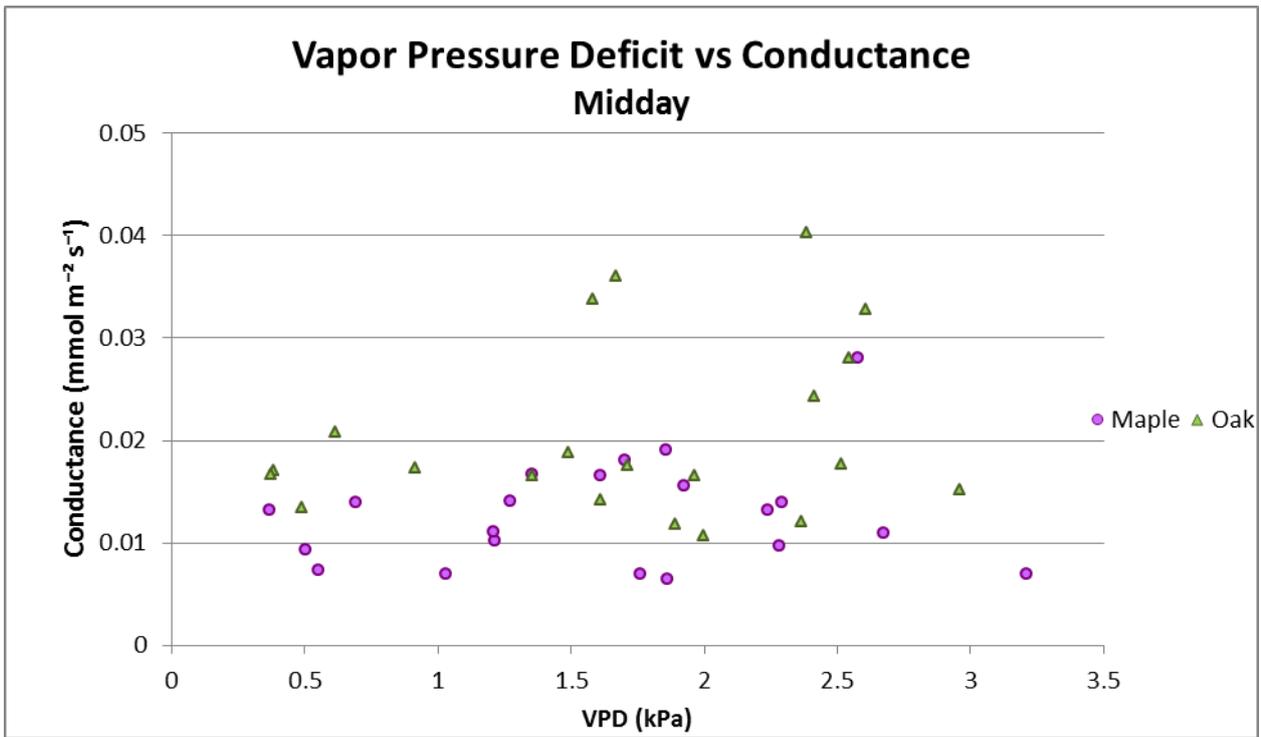


Figure 8. Midday VPD and stomatal conductance. Linear regressions were analyzed to exclude variation due to soil moisture and PAR, but this graph shows the actual measured variation; no significant relationships.

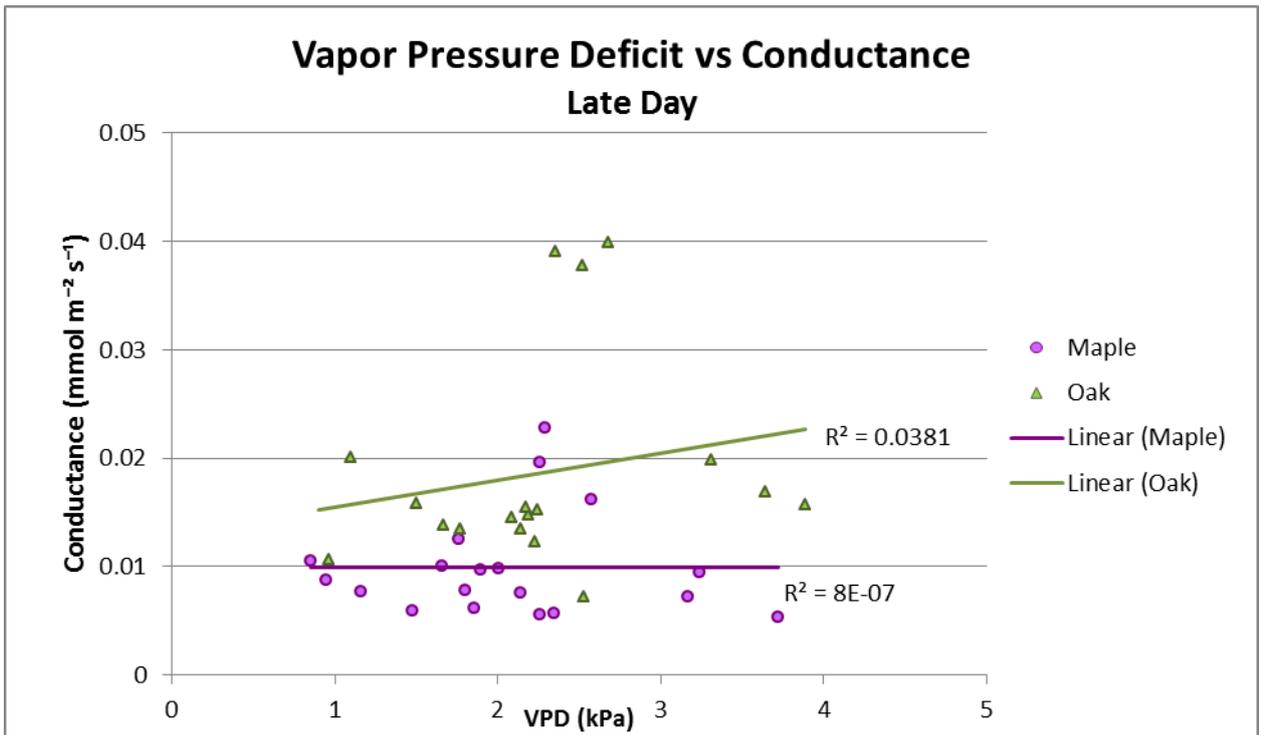


Figure 9. Late day VPD and stomatal conductance. Linear regressions were analyzed to exclude variation due to soil moisture and PAR, but this graph shows the actual measured variation; significant relationships are indicated by the presence of trend lines.

- **Conductance, PAR, and photosynthesis**

Photosynthesis was found to be highly significantly correlated to photosynthetically active radiation (PAR) ($p < .001$) (Fig. 8) and stomatal conductance ($p < .001$) (Fig. 9) with a linear regression using soil moisture, VPD, PAR, and conductance as the independent variables.

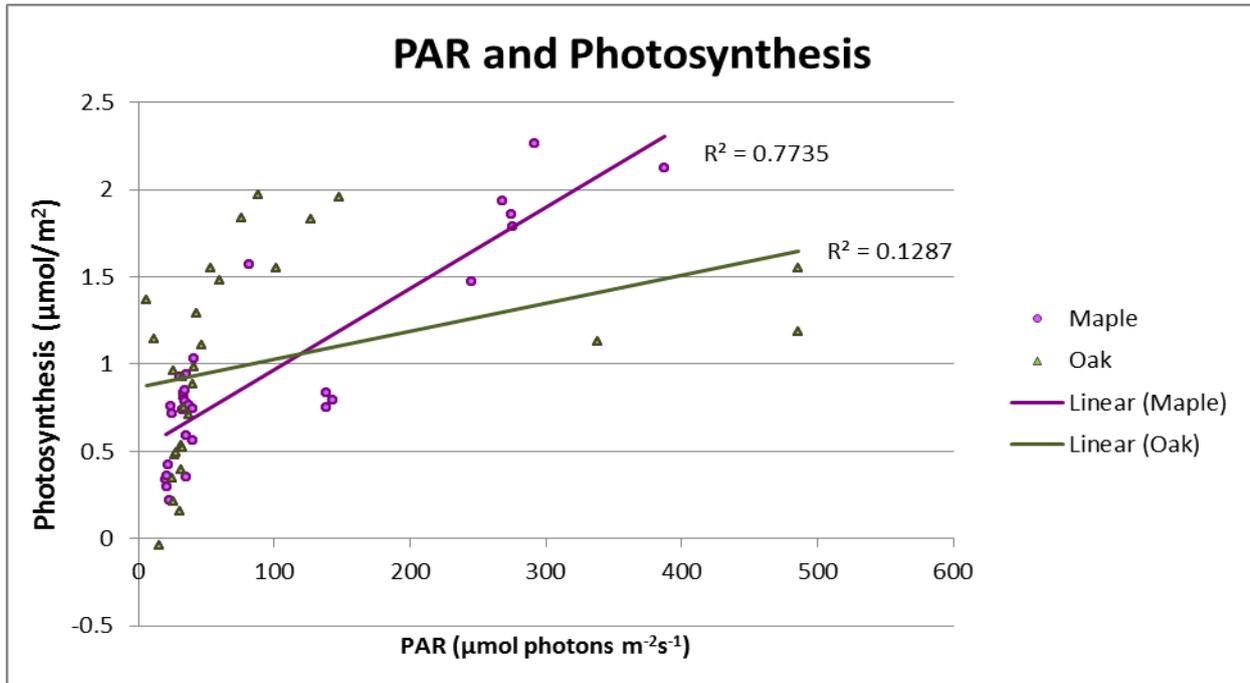


Figure 10. PAR and photosynthesis. Linear regressions were analyzed to exclude variation due to soil moisture, VPD, and conductance, but this graph shows the actual measured variation; significant relationships are indicated by the presence of trend lines.

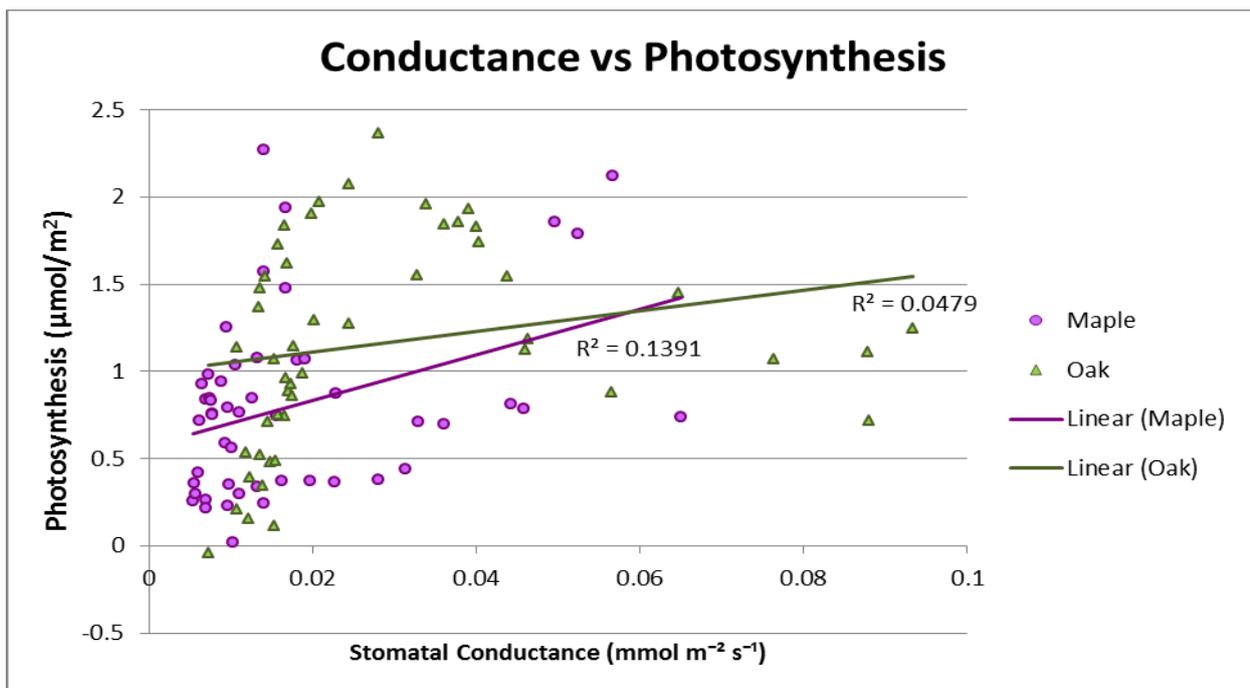


Figure 11. Stomatal conductance and photosynthesis. Linear regressions were analyzed to exclude variation due to soil moisture, VPD, and PAR, but this graph shows the actual measured variation; significant relationships are indicated by the presence of trend lines

- **Vapor pressure deficit and photosynthesis**

The relationship between photosynthesis and VPD was analyzed using linear regressions with soil moisture and PAR as additional independent variables, so that the relationship due to VPD if the other factors were held constant could be seen. During the midday time period, the relationship between VPD and photosynthesis for oaks was highly significant ($p < .000$), but the relationship for maples was not significant ($p = .165$) (Fig. 12). Late day relationships were highly significant for both maples ($p < .000$) and oaks ($p < .000$) (Fig. 13).

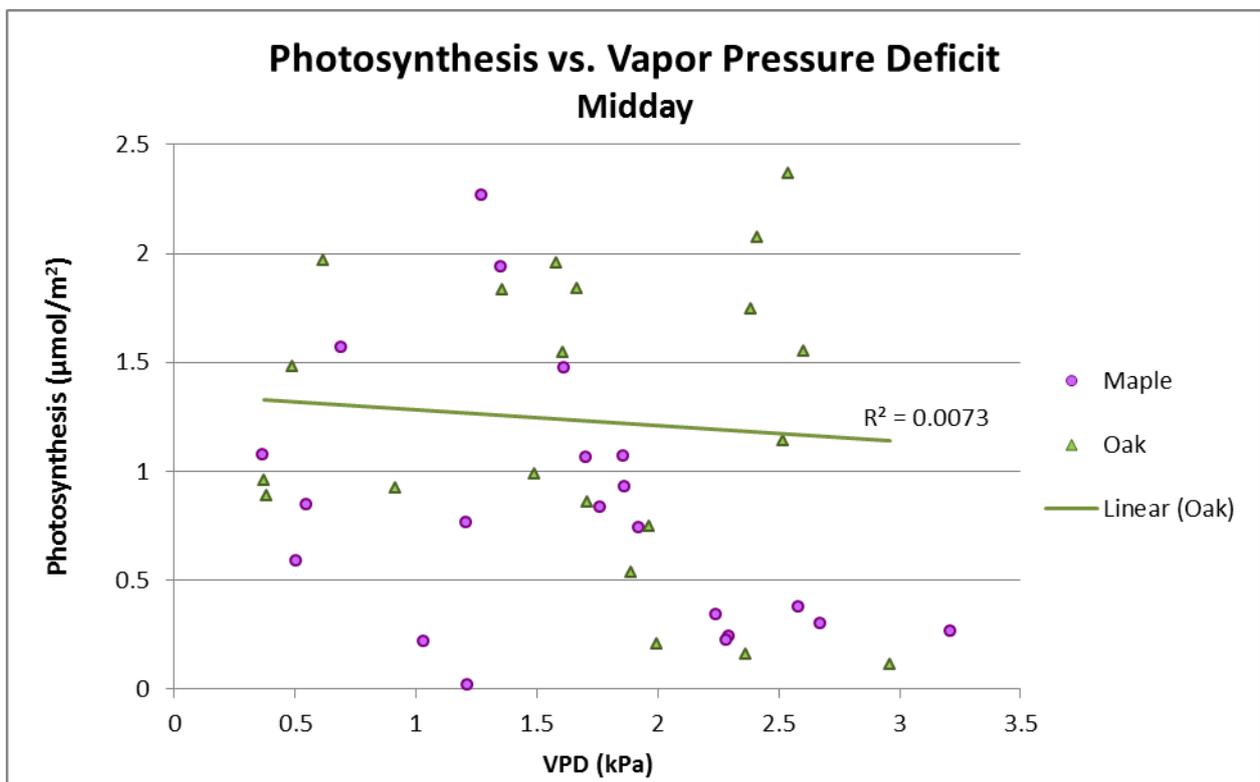


Figure 12. Midday VPD and photosynthesis. Linear regressions were analyzed to exclude variation due to soil moisture and PAR, but this graph shows the actual measured variation; significant relationships are indicated by the presence of trend lines.

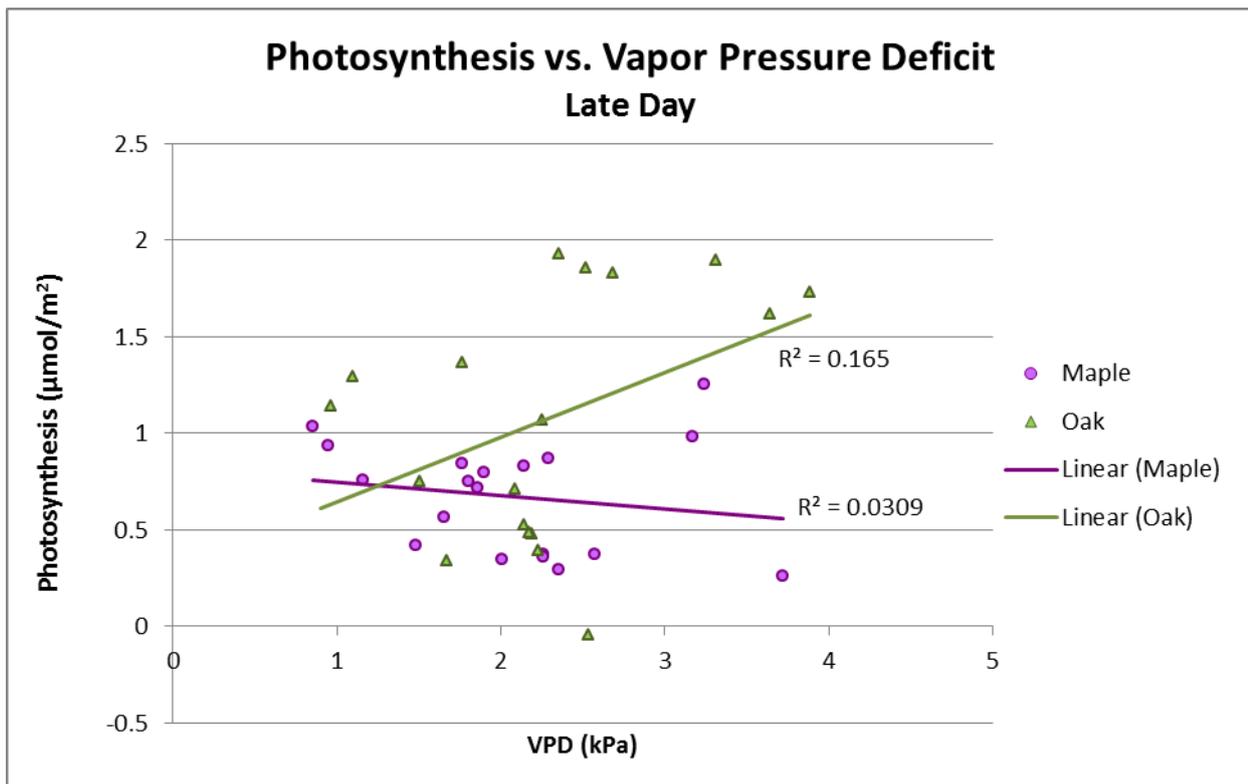


Figure 13. Late day VPD and photosynthesis. Linear regressions were analyzed to exclude variation due to soil moisture and PAR, but this graph shows the actual measured variation; significant relationships are indicated by the presence of trend lines.

- **Soil moisture and photosynthesis**

The relationship between photosynthesis and soil moisture was analyzed for maples and oaks for midday and late day time periods using linear regressions that also used VPD and PAR as independent variables so that the analyzed relationships would not include variation due to these factors. The only significant relationship between soil moisture and photosynthesis was that for oaks during the midday time period ($p=.002$) (Fig. 10). The midday relationship for maples ($p=.738$), the late day relationship for maples ($p=.260$), and the late day relationship for oaks ($p=.255$) were not significantly correlated (Figs. 10, 11).

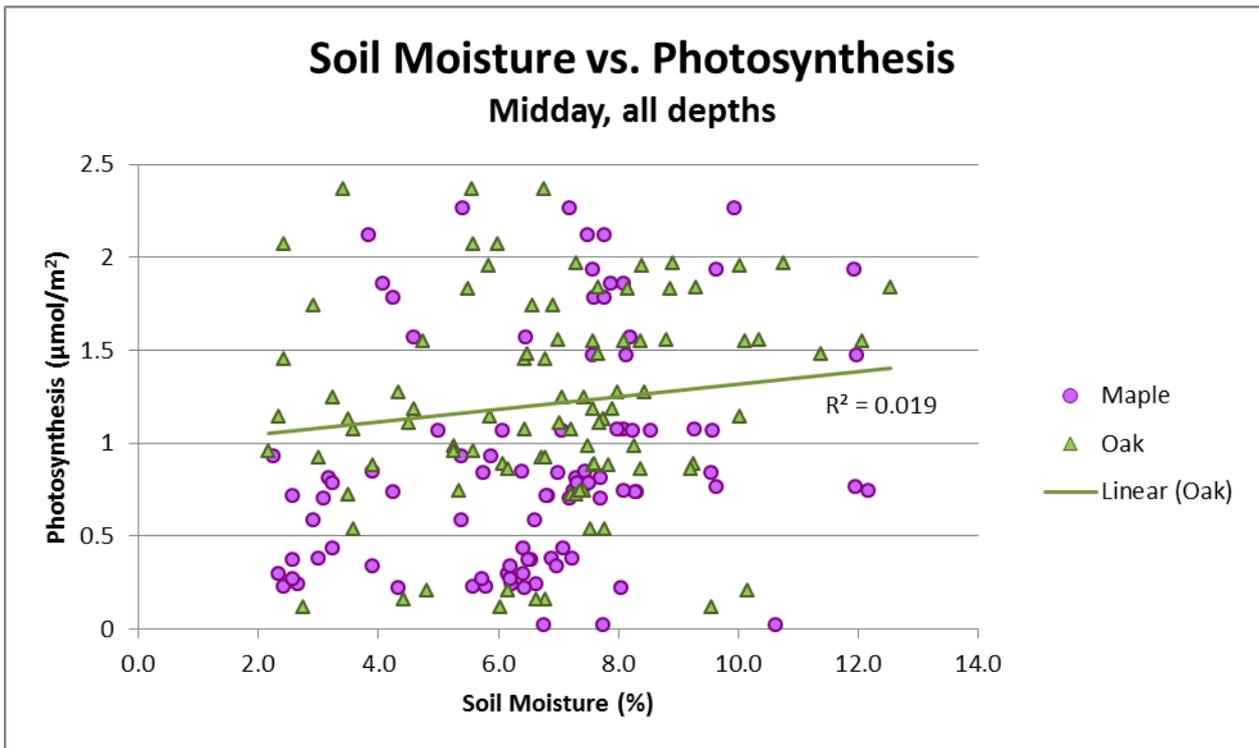


Figure 14. Midday soil moisture and photosynthesis. Linear regressions were analyzed to exclude variation due to VPD and PAR, but this graph shows the actual measured variation; significant relationships are indicated by the presence of trend lines.

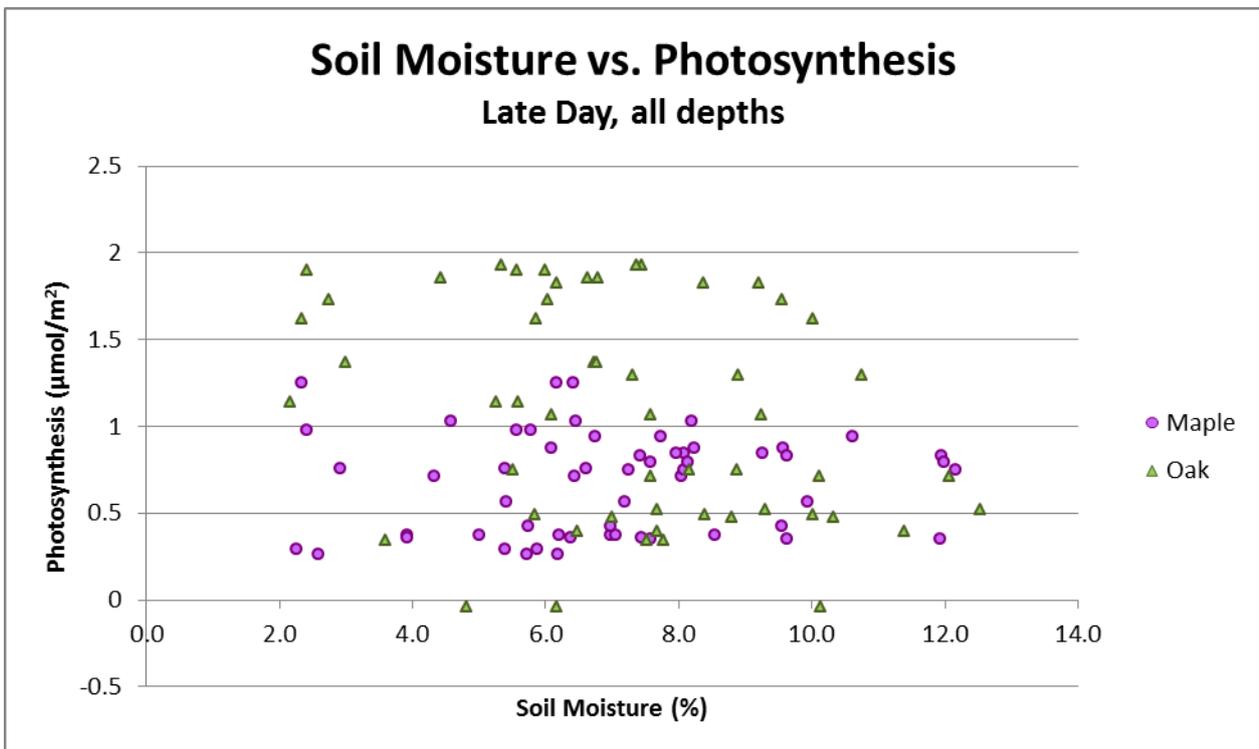


Figure 15. Late day soil moisture and photosynthesis. Linear regressions were analyzed to exclude variation due to VPD and PAR, but this graph shows the actual measured variation; no significant relationships.

Discussion:

It was expected that soil moisture would have a general negative trend over the course of the study, since over the course of a growing season soil moisture tends to decline as plant water demand becomes greater than input from precipitation (James et al, 2003). However, no such trend was seen during the study period (Fig. 1). There were several small-scale trends of high to low soil moisture between rains, but no overall trend. This could potentially be due to that fact that Pellston, MI (where UMBS is located) received more than an inch more precipitation during July 2012 (during which the majority of the measurements were taken) than the July average (Weather Underground, ret. 2012).

LWP also showed no seasonal trend, but did not exhibit the same pattern of decreasing between rains as soil moisture did (Fig. 2), indicating that LWP is more closely coupled with a different variable than soil moisture. This was supported by statistical analysis which showed that the LWP of oak trees were only significantly correlated to soil moisture during the predawn period, while maples were only significantly correlated during midday (Figs. 3-5). However, LWP and VPD were significantly correlated for both maples and oaks during both daytime time periods (Figs. 6-7); predawn relationships were not examined, because at night photosynthesis is zero, so stomata are closed, making the tree unresponsive to air moisture conditions.

When the stomata were open, though, the conductance of maples and oaks also responded similarly to differences in VPD. Both species showed significant positive correlations between conductance and VPD for midday and late day time periods (Fig. 8-9). This is unsurprising; since conductance is a measure of how much carbon dioxide and water vapor is being exchanged through stomata, and VPD is a measure of how much more water vapor the air is able to hold, it makes sense that a high VPD would increase the magnitude of the water concentration gradient between the soil, the plant, and the air, and thus increase the amount of water drawn up from the soil and out into the air. Together, the similarities of oaks' and maples' LWP and conductance responses to VPD indicate that both species have similar sensitivities to air and within-plant water relationships.

The aspen sprouts studied behaved much differently, though; aspen sprouts' LWP and VPD were not significantly correlated, unlike maples and oaks (Figs. 6-7). Additionally, there were significantly correlated relationships between soil moisture and LWP for both the midday and late day time periods (Figs. 3-5), but the relationships were negative, indicating that higher soil moisture was correlated to lower LWP, and thus plants that were under a greater amount of water stress. Although it was expected that aspen sprouts (ramets), since they get the majority of their resources from the parent tree (ortet) whose root system they are growing from (Barnes, 1966), would behave differently than independent trees like maples and oaks, this relationship does not make sense. There is no easy explanation for why increased moisture should cause plants to have lower water potential. The most likely explanation is that there is some unmeasured variable that covaried with soil moisture also affecting LWP, but it is, as yet, a mystery what that variable might be.

Although the relationships between LWP and conductance and VPD showed a rough similarity of water relationship sensitivities between maples and oaks, the two species differed in their physiological responses. When the relationship between VPD and photosynthesis was examined, a significant positive correlation was found for oaks in both the midday and late day time periods, but maples showed a significant positive correlation for only the late day period. Although the trend appears to be negative for oaks in the late day period, the trend becomes positive when variation due to PAR and soil moisture are statistically removed (Figs. 12-13). This difference in responses indicates that maples are more conservative with their water use than oaks.

This is strengthened by the differences in the relationship between photosynthesis and soil moisture for the two species. The only significant correlation found was for oaks at midday; the relationship for maples was not significant for either time period (Figs. 14-15). The similarity of VPD and LWP responses of maples and oaks along with the differences in photosynthesis responses indicates that maples more closely regulate their metabolic processes, keeping processes such as photosynthesis fairly constant regardless of water availability. Oaks, on the other hand, increase their rate of photosynthesis much more dramatically. This has the effect of causing the LWP of oaks

to drop to lower levels than occurs in maples. However, this does not necessarily indicate that oaks experience more moisture stress than maples do, just that they are more responsive to differences in moisture levels. The level of LWP that causes stress differs across species, since resistance to xylem cavitation (pockets of air in the xylem, which is caused by, among other things, extremely low xylem water pressure, and makes water flow within a plant very difficult; if cavitation is too extreme, it can be fatal) differs greatly between species (Maherali et al, 2004). The air and soil moisture conditions measured in this study did not drop low enough to observe significant moisture stress in either species.

The responses of maples and oaks represent two opposite water use strategies used by plants. Maples avoid water stress by tightly regulating transpiration (by closing stomata and shutting down photosynthesis when VPD is too high) and thus avoid potentially damaging low water potentials; this strategy is called isohydric. Oaks, on the other hand, are an anisohydric species—they keep their stomata open (and, thus, transpiring and photosynthesizing) for much longer periods of time than isohydric plants; this has the benefit of allowing the plant to continue to produce carbohydrates for a greater amount of time, but also contains the risk of damaging cells, portions of tissue, or even the whole plant via cavitation-induced dehydration if water availability remains too low for too long (Sade et al 2012).

The differences in these two strategies could become huge as climate change continues and the frequency and severity of droughts continues to increase. Under periods of moderate drought, the anisohydric strategy tends to be more beneficial, since it allows plants to uptake more resources. However, it is unclear which strategy wins out during prolonged periods of intense drought. On the one hand, anisohydric plants are able to store more carbohydrates than isohydric plants, so they may be better able to withstand periods where photosynthesis is essentially zero (such as winter). On the other hand, isohydric plants might be more resistant, since they are more conservative with their water use and thus may be less likely to have their water potentials drop to fatal levels.

These differences are also very relevant to climate modeling; a forest that is made of mostly

anisohydric trees will respond much differently to drought than one with mostly isohydric trees, which will have a dramatic impact on the proportion of CO₂ removed from the atmosphere to that given off by respiration, and thus an impact on the change in mean global temperature. Future research that studies how these two strategies fare in droughts that are prolonged and intense will be critical to more effective forest management as well as better understanding and modeling forest-atmosphere interactions as the climate continues to change.

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